DISTURBANCE, RESOURCES, AND EXOTIC PLANT INVASION: GAP SIZE EFFECTS IN A REDWOOD FOREST

Brent C. Blair[1], Deborah K. Letourneau, and Sara G. Bothwell
Department of Environmental Studies, University of California, Santa Cruz, CA 95064
blairb@xavier.edu

Grey F. Hayes
Elkhorn Slough National Estaurine Research Reserve, Watsonville, CA 95076

Abstract

Fluctuations in plant resource availability are hypothesized to promote exotic plant invasion by allowing propagules already present in an area a chance to successfully compete for unused resources. To examine the relationship between resource enrichment and exotic species invasion, we used selective logging canopy gaps over a range of sizes (56 m^2 to >1500 m^2) in a redwood forest (Santa Cruz County, CA) as a surrogate for disturbance intensity and level of pulsed resource enrichment. Measurements of abiotic conditions in gaps ca. 10 yr after logging suggest light is the primary difference in current resource availability, though a pulse of light and nutrients likely occurred at the time of gap formation. Exotic species richness and relative cover increased significantly as gap size increased. In a separate manipulative experiment, we compared understory plant composition between artificially shaded and unshaded plots in 2.5-year-old logging gaps. Shaded plots had a lower proportion of exotic species than did adjacent, unshaded plots, showing that light is a critical resource for exotic species in redwood forest habitats. Taken together, these results support the view that both physical disturbance and increased availability of scarce resources contribute to a community's susceptibility to invasion and suggest a linear relationship between the size of logging gaps and the magnitude of exotic species invasion.

Key Words: Canopy gap, disturbance, redwood forest, selective logging, *Sequoia sempervirens*, understory.

The probability of invasion by non-native plant species is determined by the supply of introduced propagules, the capacity of these species to establish, and the susceptibility of the environment to invasion (Lonsdale 1999). Susceptibility, or invasibility, of the environment is determined by bottom-up forces (such as light and nutrients), top-down forces (such as herbivores and pathogens) and lateral forces (facilitative and competitive interactions among plants) (Davis et al. 2000). Theories on invasibility often focus on the dynamics of bottom-up forces and suggest that increases in resource availability (e.g., light, moisture, nutrients) promote invasibility of plant communities. For example, increased water supply in drought-prone areas often promotes invasion (Li and Wilson 1998; Davis et al. 1999; Dukes and Mooney 1999) as does the addition of limiting nutrients in North American grasslands (Stohlgren et al. 1999). Alternative theory suggests that physical disturbance acts by disrupting existing species interactions, diminishing the competitive intensity for resources within plant communities, and thus allows foreign invaders to take a foothold (Rejmanek 1989; Hobbs and Huenneke 1992).

Disturbance may also increase unused resources in a community by disrupting resource uptake. Davis et al. (2000) suggest that it is the presence of unused resources rather than total amount of resources that is critical to invasive species success.

While studies confirm that both physical disturbance and changes in resource availability promote exotic species invasion (Li and Wilson 1998; Stohlgren et al. 1999; Rodgers and Parker 2003; Glasgow and Matlack 2007), the magnitude of change attributable to each of these factors is rarely studied. However, we know that plant competitive intensity declines as the magnitude of unused resources increases (Davis et al. 1998). Therefore, a large increase in resource availability should boost the success of exotic species invasions.

Canopy gaps caused either by natural treefalls or logging events are one type of disturbance that increases local resource availability. Canopy gap formation causes an immediate resource pulse at the forest floor. The quantity and quality of light increase proportionate to the amount the overstory shade is diminished (Collins et al. 1985). Higher precipitation throughfall and lower transpiration may cause soil moisture to increase (Collins et al. 1985), but this trend may be mediated in areas with coastal fog (Dawson

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[1] Present address: Department of Biology, Xavier University, Cincinnati, OH 45207.

1998). Soil disturbance caused by fallen or extracted trees can also create a mineral soil seedbed critical for plant germination (Battles et al. 2001). Decaying plant debris from fallen or extracted trees, in combination with reduced plant uptake, increase nutrient availability (Matson and Vitousek 1981; Vitousek 1985a, b; Frazer et al. 1990). Eventually these abiotic resources return to base levels, but return time varies among these resource classes and could be quite long in areas where soil mineralization rates are low. Surplus nutrients that are not absorbed by rapidly colonizing plants are lost, in the relatively short term, through erosion and leaching (Uhl et al. 1982; Vitousek 1985b). Similarly, excess soil moisture and newly formed mineral soil seedbeds will decline as plants and their roots re-colonize empty space above and belowground. However, light levels decline slowly and canopy closure may take years or decades to complete (Moore and Vankat 1986). Thus, canopy gaps cause a resource pulse whose components re-equilibrate at different rates.

Canopy gaps cause measurable changes in herbaceous species composition in forest ecosystems (Davison and Forman 1982; Moore and Vankat 1986; Glasgow and Matlack 2007). Moore and Vankat (1986), for example, found that while total species richness remained unchanged in canopy gaps, species composition changed substantially with early spring annuals declining and late spring and summer species becoming more abundant. California's coastal redwood forest communities tend to be composed of native species, with low light levels in the understory providing a potential barrier to colonization by the many exotic plants that thrive in disturbed sites in the region. Selective logging events are different than natural treefalls as they remove large merchantable tree boles while unmerchantable stumps, branches and leaf litter remain. Experiments using selective tree removal have found that changes in understory plant composition are similar to those in natural treefall gaps of similar size (Collins et al. 1985; Collins and Pickett 1988a).

We conducted two complementary field studies using canopy gaps formed during selective logging to examine the effects of physical disturbance (tree removal) and resource pulses on exotic species invasion in a coast redwood (*Sequoia sempervirens* (D.Don) Endl.) forest. In the first study we used forest canopy gaps of different sizes that were created in the 1990's by selective logging operations to examine the effects of logging disturbance magnitude on invasibility in the understory plant community (referred to as the *gap size* study). Gap sizes in this study encompassed a range of over an order of magnitude in area (56 m² to 1612 m²) and were of similar size to natural treefalls found in

redwood forests (160 m² to 1770 m²) (Sugihara 1992; Busing and Fugimori 2002) as well as other temperate forests (8 to 1320 m²) (Barden 1981; Romme and Martin 1982; Collins and Pickett 1988b). In the second study we tested for a direct effect of light as a pulsed resource after logging by using paired, artificially shaded (using shade cloth) and unshaded plots in newly created logging gaps in the same forest (referred to as the *light effect* experiment).

In these studies, we tested the hypothesis that exotic plant species survival and dominance are positively influenced by physical disturbance (tree removal) and resource pulses (light and nutrients) created by gap formation during selective logging. We predicted that exotic species richness and cover would increase concomitantly with the size of canopy gap, in the gap size study. In the light effect experiment, we expected that sections of canopy gaps covered by shade cloth would experience a reduced influx of exotic species after gap formation when compared to unshaded regions of the same canopy opening.

Methods

Study Site

For both experiments, we used selective logging sites in a redwood forest located in the Santa Cruz Mountains at Swanton Pacific Ranch, ca. 21 km north of Santa Cruz, CA (37°04'N. 122°14'W), a 3200 acre property owned and managed by the California Polytechnic University, San Luis Obispo. The region receives approximately 700 mm of rainfall annually, mostly between November and May, and has a mean temperature of 13C. The forest, which was clear-cut in the early 1900's, is dominated by coast redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). In 1991 and 1995, California Polytechnic designated forest sections to be selectively logged. They removed individual and small stands of trees, leaving canopy gaps of various sizes scattered within the forest. For the gap size comparison, we established 16 understory plant census plots (8 × 8 m) in clearings under canopy gaps. All gaps were located in an area of ca. 0.5 km² (Fig. 1). Gaps were identified through a comprehensive search of the logged area and all gaps over 100 m² were used. The shade cloth experiment was established in two sections of the same forest, after a third selective logging operation completed in November 2004. These sections were not affected by the 1991 or 1995 logging events. For this second experiment, we established paired plots (shaded and unshaded) in 14 clearings under logging gaps.
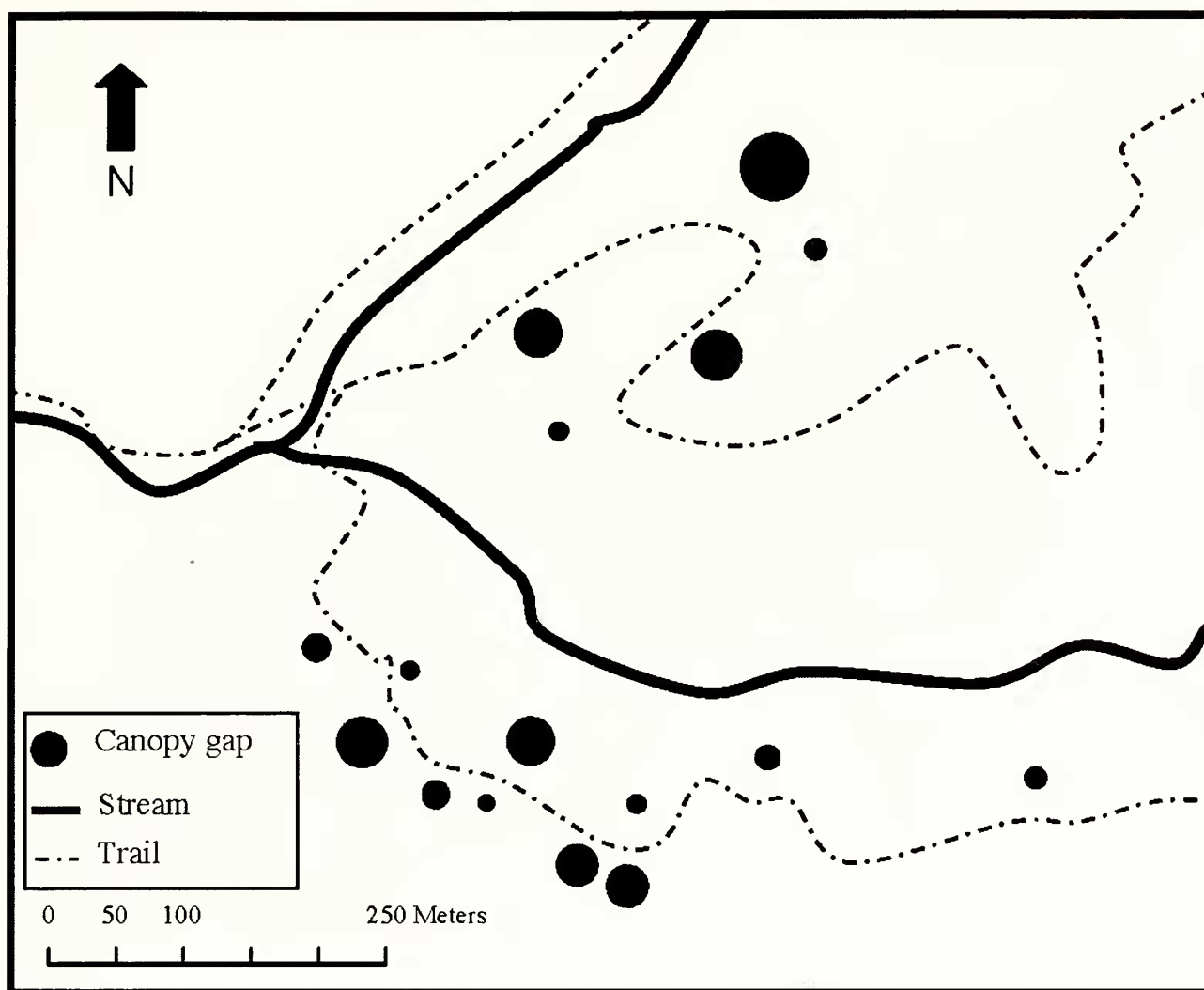
FIG. 1.   The location of canopy gaps at Swanton Pacific Ranch (n = 16) used in gap size comparison are represented by black circles showing relative sizes and proximities.

Gap Size Effects

Plot evaluation. For the gap size comparison, gaps were initially identified as clearings of >100 m² with no mature tree stems. Canopy gap openings were measured in each of eight compass directions as the distance from plot center to points directly below the edge of surrounding canopy foliage (Brokaw 1982). Hemispherical photographs were taken with a Nikon 6006 camera (Nikon, Melville, NY, USA) and a Peleng 8-mm fisheye lens (Peleng, Minsk, Belarus) using Kodak Elite-Chrome film (200 ASA, Eastman Kodak, Rochester, NY, USA). The camera was mounted on a tripod, pointed skyward, and positioned so that the top of the photograph corresponded to due north. After leveling the camera, two photographs were taken at each plot. The photograph at each site with the best contrast was used for analysis. Slides were digitized using a Polaroid Sprint 35 mm scanner (Boston, MA, USA). Images were then analyzed using the computer program Gap Light Analyzer 2.0 (Frazer et al. 1999) to determine percent transmitted global photosynthetically active radiation (PAR). Percent transmitted PAR represents the amount of above-canopy direct and diffuse PAR incident beneath the canopy (Canham 1988).

To determine temperature and humidity we placed data loggers and probes (Campbell, Logan, UT, USA) at the center of six plots that represented the range of gap sizes present in this study. We measured temperature and relative humidity in five plots and temperature in the sixth between July 18 and September 17, 2003. This period represents the warmest and driest weeks of the year (Mediterranean climate) when temperature and humidity differences between small and large gaps should be most pronounced. Data loggers calculated minimum and maximum daily temperature and relative humidity. We conducted linear regression analysis (SPSS 1999) to determine the effects of gap size on temperature and humidity.

Soil properties. To determine if soil moisture (surface and root zone) varied with gap size in the wet and dry season we measured water content in each plot, using two 5 cm-diameter soil cores from a 0–5 cm and 5–20 cm depth in June (dry season) and November (wet season), 2003. Fresh 10 g sub-samples from each core (4 per plot) were oven dried at 90C to constant weight and subsequently weighed to calculate water content. The levels of essential plant nutrients (N, P, K, Mg and Ca) in the plots were determined from the remaining soil in the 0–5 cm cores. These

samples were air dried and passed through a 2 mm sieve. The two dried 0–5 cm soil samples from each plot were pooled and mixed thoroughly before analysis for available N (nitrate and ammonium), P, K, Mg and Ca. Soil N, Mg and Ca were determined using soil sub-samples extracted with a sodium acetate solution and P was extracted with Bray's solution (Page et al. 1982). Soil chemical analyses were carried out at Perry Laboratories (Watsonville, CA, USA). Gap size effects on soil properties were examined using regression analysis (SPSS 1999).

Vegetation purveys. We surveyed each of the sixteen 8 m × 8 m plots in April of 2003, during the peak flowering season for understory herbs (February–May), to determine the total number of plant species and the number of exotic plant species present. We estimated plant cover for each species in the center 6 m × 6 m area of each plot, to reduce potential edge effects. Within this area, we randomly chose nine of the possible thirty-six 1 m^2 subplots. For each of the 9 subplots, a 50 cm × 50 cm grid with twenty-five 10 cm × 10 cm cells was held over the vegetation at approximately 1 m height. The number of cells (0–25) that contained a particular species served as a measure of relative cover for that species.

We quantified plant species richness and diversity by using the number of species per unit area in the whole plot censuses (S_t), and a measure of evenness (J). The index J is defined as follows:

$$ J = \frac{- \sum\limits_{i=1}^{S_t} P_i \ln P_i}{\ln S_t} ; $$

where P_i is the relative frequency of occurrence of every species in each plot's nine point-count subplots, and S_t is the total number of species in each 64 m^2 plot.

Exotic (S_e) and native (S_n) species richness were determined using the whole plot (8 m × 8 m) census data. To determine exotic species relative cover (C_c) we used the quadrat cell count data to obtain percentages for each plot. The index C_c is defined as follows,

$$ C_e = \frac{\sum\limits_{i=1}^{S_e} e_i}{\sum\limits_{i=1}^{S_e} e_i + \sum\limits_{i=1}^{S_n} n_i} ; $$

where e_i is the number of occurrences of exotic species i in the nine 25 cell grids, n_i is the number of occurrences of native species i in the nine 25 cell grids, S_c and S_n are the total number of exotic and native species found in the plot. To evaluate treatment effects on species diversity and composition we conducted regression analyses (SPSS

1999). The effects of gap size and percent canopy cover were tested on the number of exotic (S_e) and native (S_n) species, exotic relative cover (C_e), and evenness (J). The index C_e was square-root transformed prior to analysis to meet assumptions of normality.

Light Effects – Experimental Manipulations and Vegetation Survey

In April of 2004, 12 clearings (>100 m^2) under closed canopy were identified by their proximity to trees to be removed during the upcoming logging operation. We surveyed each of the clearings to determine the total number of native and exotic plant species present. After tree extraction in October of 2004, two additional clearings were added and one of the previous sites was discarded due to lack of increased light penetration at the forest floor after logging. The remaining 11 previously surveyed and 2 new clearings corresponded to areas of increased light penetration (canopy openings). Within each of the 13 clearings, we demarcated a pair of 5 m × 5 m plots, and randomly assigned the shade treatment to one plot in each pair. The remaining plot was used as an open (unshaded) control. In January 2005, shade cloth (80% shade) was suspended from a PVC frame 1.5 m in height, with a 2 m T-bar in the center to elevate the center of the shade canopy and reduce litter accumulation on the structure. Shade cloth was draped over the edges of the structure but left 1 m above the ground uncovered to allow access by arthropods and ensure airflow. Each pair of plots (shaded and open) was established within 10 m of each other within a single clearing. When on a slope, paired plots were positioned to have the same slope aspect. In July 2007, all pairs of shaded and open plots were censused for the total number of native and exotic plant species. The relative number of plant species in shade and open plots was compared using a paired t-test for equal variances on the normally distributed differences between light and dark plots for total plant species, native plant species, and exotic plant species per plot (SPSS 1999).

RESULTS

Gap Size Effects

Abiotic factors. Percent transmitted global PAR increased significantly with gap size (Table 1). Average maximum daily temperatures also increased with gap size (Table 1). However, minimum daily temperatures were similar across all gap sizes. In smaller gaps, we measured higher minimum humidity levels than in larger gaps, but maximum humidity levels were similar (Table 1).

TABLE 1.   EFFECT OF CANOPY GAP SIZE ON GAP PROPERTIES. Significant P values are indicated in bold.

Property	Coefficient	R^2	F (N)	P-value
Transmitted global PAR (%)	0.010	0.61	14.91 (16)	**0.002**
Native species richness	0.004	0.24	4.43 (16)	0.054
Exotic species richness	0.002	0.71	33.68 (16)	**<0.001**
Exotic relative cover	0.0002	0.41	9.91 (16)	**0.007**
Temperature (C°)				
Minimum	−0.002	0.32	1.89 (6)	0.241
Maximum	0.006	0.83	19.40 (6)	**0.012**
Humidity (%)				
Minimum	−0.040	0.82	13.93 (5)	**0.034**
Maximum	−0.003	0.54	3.47 (5)	0.159

Soil moisture was significantly greater during the wet season than the dry season (t = 8.11, df = 15, P < 0.001). However, sampling within each period showed no significant differences in moisture levels between gap sizes at the 0–5 cm or 5–20 cm depths. No gap size-dependent trends were found for nutrient availability.

Vegetation. The understory vegetation in selectively logged redwood forest gaps was typical of that found in natural forest. Common native species such as *Oxalis oregana* Nutt. (redwood sorrel), *Polystichum munitum* (Kaulf.) Presl. (western sword fern), *Rubus ursinus* Cham. & Schlecht (California blackberry), *Stachys bullata* Benth. (California hedge nettle), and *Trillium ovatum* Pursh. (western wake-robin) were present. The five largest canopy gaps (832 m²–1612 m²) contained between 18 to 27 understory plant species, medium gaps (212 m²–624 m²) had 15 to 26 species, and the smallest gaps (<150 m²) had between 11 and 21 species. The total number of native understory plant species in canopy gaps showed no significant relationship with gap size (Table 1) or light availability, though native species richness tended to increase with gap size (coefficient = 0.004, r² = 0.24, P = 0.06).

In contrast, the number and percent cover of exotic plant species increased significantly with gap size and light availability (Table 1, Fig. 2). The exotic plant species found in understory plots were: *Cirsium vulgare* (Savi) Ten. (bull thistle), *Cortaderia jubata* (Lem.) Stapf (jubata grass), *Erechtites minima* (Poir.) DC. (Australian fireweed), *Myosotis latifolia* Poir. (forget-me-not), *Rubus discolor* Weihe & Ness (Himalayan blackberry), *Vulpia* sp. (annual fescue), and *Torilis* sp. (hedge-parsley). The relationship between gap size and estimated light availability was strong (r² = 0.61) and both were good predictors for exotic species number (r² = 0.71 (gap size) vs. r² = 0.82 (light availability)). However, light availability was a far better predictor of exotic species relative cover (r² = 0.61) than gap size (r² = 0.41) (Table 1, Fig. 2). The exotic and native species

evenness was unrelated to either gap size (coefficient = 0.0001, r² = 0.15, P = 0.134) or to light availability (coefficient = 0.005, r² = 0.14, P = 0.147).
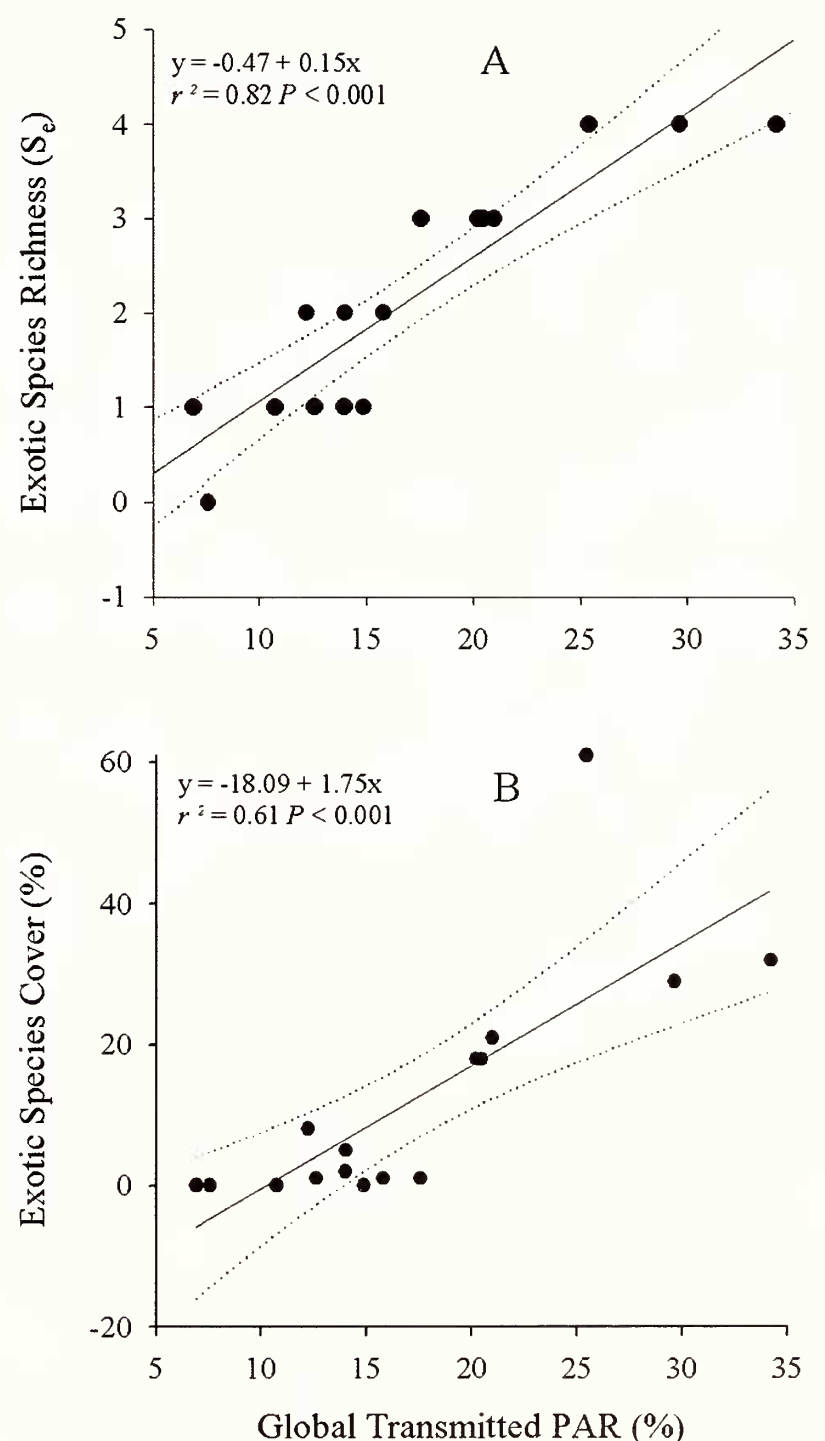

FIG. 2.   Relationship between exotic species richness (A), and exotic species relative cover (B) with global transmitted PAR (%). Dotted lines represent 95% confidence intervals.
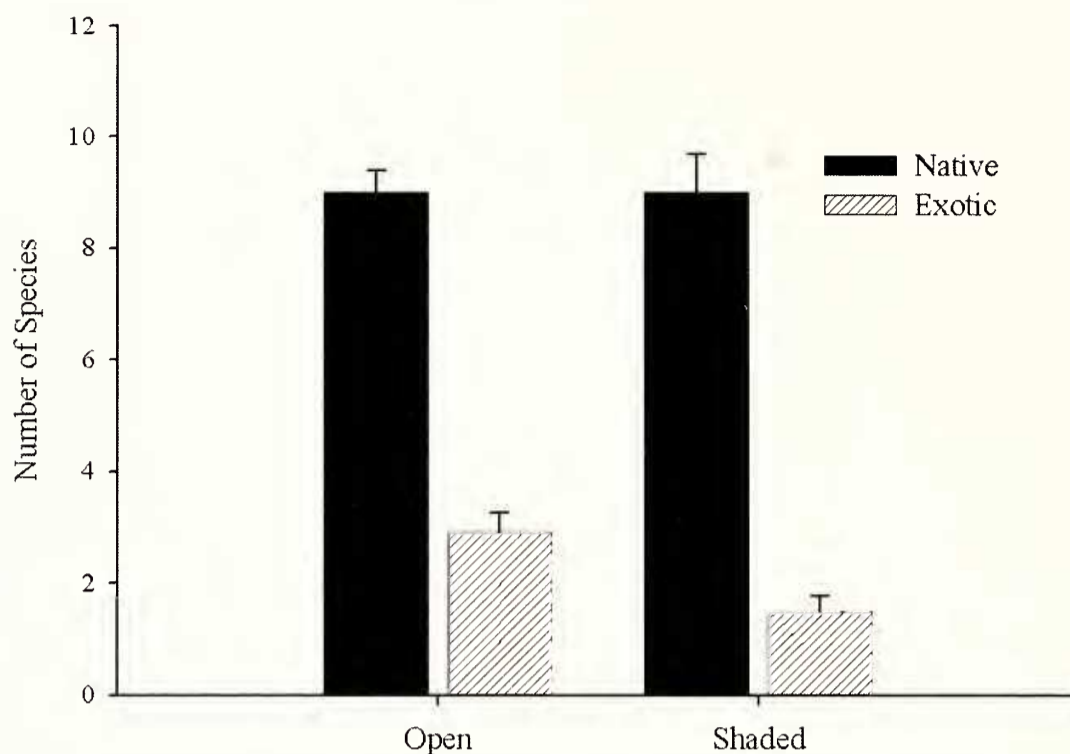
Fig. 3.   Mean native and exotic species richness (±SE) in gaps 32 mo after selective logging in artificially shaded and open plots (n = 14 pairs).

Light Effects on Vegetation

The number of plant species occurring in pre-harvest understory in April, 2004 was half the plant species richness occurring within the forest gaps comparison (above) surveyed the previous year (average of 10.3 species in closed canopy before logging versus 20 species, on average, in all gaps). Plant species richness did not increase strongly after 2.5 yr, with a mean richness of 11.9 (±0.5 SE) per 5 m × 5 m light plot (n = 14). However, in the pre-harvest samples, all the species were natives, compared to a mean of 2.9 (±0.3 SE) exotic species per 5 m × 5 m in post-logging open plots. Neither did the addition of shade cloth after logging have a significant effect on plant understory species richness or the number of native species present, on average, in the plot. However, there was twice the number of exotic species present in open plots than in shaded plots (t = −4.2, df = 13, P = 0.001) (Fig. 3).

Discussion

The increasing richness and cover of exotic plant species across selectively logged forest gaps of increasing size supports our prediction that the magnitude of disturbance positively affects exotic species invasion, directly and/or through a resulting pulse in available plant resources. The removal of individuals or clusters of timber trees resulted in direct disturbance of existing vegetation. After disturbance, the amount of light reaching the understory immediately increased and soil likely had a short-term nutrient enrichment as nutrients were released from decaying vegetation and fewer plant roots were present for nutrient uptake (Matson and Vitousek 1981; Vitousek 1985a; Frazer et al. 1990; Frazer et al. 1999). The coupling of decreased resource use by native species with increased total resource availability during the initial disturbance period would have made more resources available to exotic species, which were otherwise suppressed by understory conditions. Over a decade after logging events took place, light availability still varies significantly and directly with the size of the gap created. Invasion of these logging gaps by exotic species and the increase in exotic species richness in gaps of increasing size was likely due to this increase in light availability, and possibly other plant resources whose initial increases are no longer detectable. The persistence of these exotic species is enabled by the length of time required for canopy gaps to close, returning PAR to pre-disturbance levels.

Our shade-cloth study suggests that disturbance and light play complementary roles. There was a doubling of the exotic species richness in unshaded plots after logging compared to the number of species found in shaded plots within the same logging gaps. Further, we found an increase in exotic species even within the experimentally shaded plots compared to the undetectable level of exotic species in our pre-harvest vegetation surveys. Previous studies have found that physical disturbance has the greatest impact on a site's invasibility if it is coupled with increased resource availability (Burke and Grime 1996; White et al. 1997; Leishman and Thomson 2005). Burke and Grime (1996), for example, showed in a manipulative field experiment that, while both physical disturbance and fertilization increased the invasibility of limestone grassland, exotic species were most successful in displacing

their native counterparts when both disturbance and fertilization were present.

However, the conditions under which the exotic species in this study typically occur, and the habits of invasive exotic plants more generally, indicate that light availability may be relatively more important than the influence of disturbance itself, through the physical disruption of established vegetation. Exotic plants, whether intentionally introduced for agricultural or ornamental use (diCastri 1989) or unintentionally introduced (i.e., agricultural weeds) (Heywood 1989), tend to originate from high-light environments. It is thus not surprising that exotics tend to be light-demanding species (Fine 2002) that are shade intolerant (Mack 1996). These characteristics suggest that many exotic species may be successful invaders only after disturbances that increase light availability. Supporting this idea, research in western Oregon found greater numbers of exotic species in the understory of old-growth Douglas-fir forests than in un-thinned second growth forests with lower light availability at the forest floor (Bailey et al. 1998). Exotic species such as *Cirsium vulgare*, *Erechtites minima*, and *Rubus discolor*, found in our study, are shade intolerant and, when found in undisturbed forests, are gradually out-competed by shade tolerant understory plants (Amor 1974; Muldavin et al. 1981; McDonald and Tappeiner 1986).

The importance of treefall gaps in forest ecology is well known. However the impacts of tree harvest on plant community structure and diversity are not clearly understood in Mediterranean forests. In late successional forests, selective logging is often one of the preferred forest management methods because it more closely emulates natural disturbance patterns in uneven-aged forests and maintains mature forest structure (Webster and Lorimer 2002). Studies find selective logging to be superior to other more disruptive management systems (e.g., clearcut and shelterwood logging) in minimizing exotic species colonization (Battles et al. 2001). Unfortunately, several studies suggest that selective logging is disruptive in subtle and indirect ways. For instance, regeneration of certain species is greater with natural gaps rather than logging gaps (Nagaike et al. 1999). Other critics cite the obvious problems and damage that occurs through the tree extraction process (Vasiliauskas 2001) and creation of logging roads and trails (Kreutzweiser and Capell 2001). Old logging roads and trails at our site may serve as pathways for propagules of exotic species into and through the redwood forest habitat (Costa and Magnusson 2002), which can then establish when even low-impact logging techniques are applied.

Perhaps a more pertinent framework is to consider how the forest as a whole responds to artificial gaps in the long term. Even a decade after gap formation, we found obvious vegetative differences among gaps of different sizes. Logging-induced changes in understory species composition are sometimes long-lived (Duffy and Meier 1992; Meier et al. 1995) and forests often revert slowly to their original structure over the course of decades or longer (Alaback and Herman 1988; Halpern and Spies 1995; He and Barclay 2000). In an unlogged forest, succession between periods of natural disturbances (wind, fire) would bring the forest back to its original vegetative composition as shade-tolerant species gradually outcompete the light demanding ones that came in after disturbance. However, because exotic propagules are likely ubiquitous in remaining redwood forests, logging gaps may well be more likely to experience long-term shifts towards exotic composition than natural, pre-invasion treefall gaps.

Exotic plant species are a ubiquitous component of terrestrial ecosystems today, and one that often negatively influences natural habitats (Vitousek et al. 1997). A range of impacts has been documented to occur in terrestrial systems (see Levine et al. 2003 for review). The impact of exotic species in the redwood forest understory is unknown, but their spread in logging gaps may change hydrology, mycorrhizal composition, and interrupt regeneration of disturbance-dependent native species, possibly leading to their extinction. Although exotic species will likely decline locally as gap closure occurs, at a larger spatial scale exotic species are a permanent component of this forest ecosystem. Exotic plants can be expected to take advantage of logging-induced canopy gaps within the forest, highlighting the importance of research on how exotic species impact forest community function. The next step, should their effects be detrimental, would be to explore ways to reduce exotic species spread. Washing logging equipment to limit the spread of exotic seeds, for example, may be a cost effective method to reduce propagule pressure during logging operations (Brooks 2007). While it is inevitable that some form of logging occurs in most publicly and privately held redwood forests, improved methodology could reduce the impact of forest management both by minimizing disturbance and diminishing propagule pressure on forested lands.

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